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Observation on the Rate of Growth of the Shell of Lake Dwelling Fresh Water Mussels.

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I. —INTRODUCTION AND STATEMENT OF PROBLEM.

Nearly all our present knowledge of the rate of growth of fresh water mussels is confined to studies of the development of juvenile mussels through the period of infection by the *glochidia* upon the host fish to a time not exceeding six years thereafter, the rate of growth of the animal being most conveniently determined by the rate of growth in length of its shell. Portions of these studies having a direct bearing upon the subject of this paper are now cited.

Curtis and Le fevre, (14), indicate that juveniles of *Lampsilis ventricosa* first observed in the second year of free life, may nearly double in size by the close of the fourth year of growth. Coker, Shira, Clark and Howard, (2), reporting upon pond raised specimens of *Lampsilis luteola* remark that four additional growing seasons are required for such shells to double in length after the second growing season. *Lampsilis gracilis*, a thin shelled species, was found to increase in length at the rate of about 190% a year. They add that since these species are all mussels of river habitat, it can not be assumed that growth in ponds is representative of the rate of growth in a natural environment. They then record an experiment with principally thick shelled, (*Quadrula*), mussels, which were placed in a crate in the Mississippi river for nearly one year. None of these mussels were over three inches in length, and after 10 months and 12 days had increased in length as follows: *Q. ebenus*, 3%; *Q. pustulosa*, 5%; *Q. metanевра*, 9%; *Q. plicata*, 8%; *Q. undata*,

24%. While granting that the conditions of the experiment were somewhat unfavorable to growth, an impression gained by these investigators was that thick shelled mussels, after they are half-grown, increased in size at the rate of $\frac{1}{4}$ in. a year or less. In summary, they state that the rate of increase in length of fresh water mussels varies from $\frac{1}{2}$ -2 inches in "paper shells," (*Lampsilis laevissima*), to $\frac{1}{4}$ in. more or less in the "niggerhead," (*Q. ebenus*), and related shells, while an intermediate rate of $\frac{3}{4}$ in. or 1 in. per year characterizes the muckets and pocketbooks, (*L. luteola* and *ventricosa*), with a slightly more rapid rate for the yellow sand shell, (*L. anodon-toides*).

Isely, (10), made a notable experimental study of the growth and migration of fresh water mussels. He collected some hundreds of mussels of various species, and after properly marking them and making necessary records as to their weight and dimensions, he returned them to their usual environment, reclaiming specimens at intervals for further observation. For 12 specimens of *Q. lachrymosa*, *undulata*, *pustulosa*, *rubiginosa*, he finds an average per cent of aggregate gain of 13% in length, $12\frac{1}{2}\%$ in height, 14% in breadth. Other data set forth by him will be referred to in discussion of the individual species dealt with in this paper. Howard, (9), attacks the problem of the growth of fresh water mussels from a broad biological standpoint. The length of juveniles of *L. luteola* growing in a floating crate at the end of the first growing season was observed to be 128 times that of the original juvenile at the beginning of free life. Depending most probably upon the conditions of the season, by the end of the second summer, these juveniles were found to have increased from 212-475% in length. As previous investigators had found, he observed that maximum growth was not attainable under the best artificial conditions of culture. All these investigators agree that growth is most rapid in the juvenile period, decreases noticeably with age, in advanced years being almost imperceptible.

It has probably become evident to the reader that the methods devised for the culture and propagation of mussels are so recent that at the present time and for some subsequent period, they will be unable to throw any light upon the rate of growth of these animals in their later years. For this reason, I believe that certain data of mine will upon analysis with fair qualifications add to our knowledge

of the rate of growth of certain species, particularly for that period after the juvenile stages. Additionally, the present paper contributes further to a series of biometric studies of mussels in relation to their environment inaugurated by Ortmann, (16), continued by the writer, (3-8), and by Ball, (1), in a recent paper.

II.—LIST OF SPECIES AND SOURCE OF MATERIAL USED.

The material studied consisted of juvenile and adult specimens of the following species, which are listed in conformance with the recent changes in the nomenclature of the Naiades sponsored by Ortmann and Walker, (17). The older name by which certain of them are known is indicated in parentheses.

1. *Fusconaja flava parvula* (Grier).
2. *Amblesma plicata* (Say).
3. *Pleurobema coccineum pauperculum* (Simpson).
4. *Elliptio dialatus sterkii* (Grier).
5. *Lasmigona* (*Symphynota*) *costata eriganensis* (Grier).
6. *Anodonta grandis footiana* (Lea).
7. *Leptodea* (*Paraptera*) *fragilis* (Raf.).
8. *Proptera alata* (Say).
9. *Anodontoides ferrussacianus subcylindraceus* (Lea).
10. *Ligumia* (*Lampsilis*) *recta* (Lam.).
11. *Lampsilis siliquoidea* (*Luteola*) *rosacea* (DeKay).
12. *Lampsilis ovata canadensis* (Lea).

The species listed represent well defined varieties of the parent Upper Mississippi species, (3, 7). They were collected by Dr. A. E. Ortmann of the Carnegie Museum in Lake Erie over a number of years, (1903-07), for a study of this kind, and are now in the collection of the Museum. Most of them were obtained at Presque Isle Bay, but a smaller amount came from La Plaisance Bay and Cedar Point. I am indebted to Dr. Ortmann for the use of the material, as well as to the authorities of the Museum for the fullest use of its facilities.

III.—PHYSICAL CONDITIONS AND TYPE OF MUSSEL FAUNA.

The type of mussel fauna has already been admirably treated in papers by Walker, (18), and Ortmann, (15). These and the physical conditions concerned have already been discussed fully by the writer elsewhere, (7), the latter being ably given for Lake Erie by Jennings, (11). For sake of convenience, however, the outstanding points concerning the physical conditions are given in the following

contrasting columns, when the relation of the lake environment to this problem will eventually become clearer.

LAKE ERIE

Water colder than in Upper Ohio, with more even regulation of temperature. Currents much less rapid than in streams, water less agitated except by moderate currents carrying but little sediment. Bottom composed of pebbles, sand, or a mixture of these depending on region of lake, with coarser sediment derived from wear of land. Temperature conditions favor more uniform production of food, while the water contains more lime.

UPPER OHIO DRAINAGE

Water warmer than in L. Erie, greater extremes of temperature. Streams more rapid than currents of L. Erie and more greatly agitated, frequent falls and rapids, short stretches of quiet pools. Rivers carry a load of debris, moving quickly over the bottom, consisting of mud, glacial till, cobbles. Food conditions, (due to extremes of temperature), are less stable, even if at times, food is more abundant.

It may be noted here that Lake Erie varieties of shells as a whole possess brighter and clearer colors than their parent shells of the Upper Ohio and Upper Mississippi; are exceptionally polished, and otherwise characterized in distinction by *their well developed lines of growth*. It has also been suggested that certain depauperate qualities of these shells, such as their dwarfed condition and thinness, may be due to the chemical quality of the water, (5), the influence of brackish water upon fluviatile species being well known.

IV.—METHOD.

A common method of estimating the age of a mussel has been to count the so-called rings or lines of growth. Studies by previously mentioned investigators, (10, 2), have shown that under certain conditions such a procedure would yield an unreliable estimate of the animal's age. For example, mussels living in rivers undoubtedly form a growth ring every winter, but what was not certainly known, was that a period of summer drought, or even temporary removal from the water, would cause a superficially similar reaction, and so far as estimating age was concerned yield misleading results.

As will be observed in the section dealing with physical conditions, not all bodies of water present the extreme conditions in relation to mussel life as those possessed by the rivers. Conditions are seen to be fairly uniform in Lake Erie, and such could be conceded to favor uniform conditions of growth. This being the case, the number of rings of growth on the shell could be reasonably conceived to represent the number of years the animal has lived.

Previously, this and other data had been gathered while making a study of the morphological characteristics of mussel shells inhabiting Lake Erie, (7), and there but remained the task for the present paper of regrouping the data chronologically, when percentages indicating the rate of growth based on the more commonly taken measurements of the shell—length, height, and inflation, as well as others not commonly made, could be calculated. A detailed description of the method of making these measurements is given in the paper cited, but for the convenience of the reader they are stated to consist of the following:

1. Length, *L*.
2. Dorso-ventral diameter, (height), *DVD*.
3. Dextro-sinistral diameter, *DSD*, (breadth).
4. 5. Distance anterior, (*AD*), and posterior, (*PD*), from *DVD*, to extremities of valve, the sum giving the total antero-posterior dimension.
6. 7. Length of anterior, (*AHL*), and posterior, (*PHL*), part of hinge measured from the beak, giving total hinge-length.
8. Thickness of valve just superior to the pallial line in the region beneath the umbo. The measurements and calculations made from them constitute the results.

V.—RESULTS.

In the following tables, each species is first dealt with separately. The ages indicated were obtained by counting the lines of growth on each specimen. In the two columns to the left are indicated the number of specimens used for an estimated age. The remaining columns contain first, the mean of the measurements described above and expressed in centimeters for the youngest juvenile of the species available. The rest of the columns consists of the mean of the dimensions of juveniles and mature shells of succeeding ages expressed in percentages of the corresponding dimensions of the youngest juvenile. The comparisons, etc., following the tables of percentages for each species are based most largely on the average of these percentages for the probable number of years represented by the series of material of that species. At other times, however, conclusions taken are based upon direct inspection. All percentages expressed are an index to the amount of growth in a particular part of the shell for the time stated. Finally, for the convenience of both reader and writer in making a comparative study of the rate of growth in different species,

the important data for each species is summarized in the table on "Comparative Growth of Species Studied," following the individual discussion of species.

1. FUSCONAJA FLAVA PARUOLA

No. Spec.	Age	L.	DVD	DSD	PD	AD	PHL	AHL	TH.
		1.7cm.	1.3cm.	.7cm.	1.3cm.	.4cm.	.75cm.	.4cm.	.13cm.
1	2	180%	180%	220%	170%	190%	200%	150%	170%
3	3	180%	192%	257%	172%	207%	188%	150%	170%
4	4	193%	198%	228%	177%	212%	213%	185%	161%
4	5	282%	295%	360%	286%	250%	333%	205%	207%
4	6	290%	290%	377%	300%	247%	318%	270%	220%
4	7	323%	321%	414%	354%	210%	400%	275%	230%
4	8	315%	309%	401%	340%	297%	373%	300%	200%
2	9	305%	340%	374%	323%	250%	386%	312%	161%
2	10	299%	330%	410%	317%	250%	333%	250%	230%
2	11	355%	347%	464%	400%	212%	500%	300%	292%
Average growth per year in each dimension for 12 years.									
		143%	150%	209%	161%	110%	192%	116%	87%

DEDUCTIONS FROM TABLE OF PERCENTAGES AND REMARKS.

In this species, increase in the various dimensions of the shell is greatest in later years. The increase in *DSD*, *PHL* and *L* is the greatest, *TH* the least. *AD* and *AHL* increase uniformly. From years 8-11 inclusive, *DVD*, *DSD*, *PD*, *PHL*, and *AHL* increase more rapidly than from 4-7 inclusive. The increase in thickness is less marked in later years, while that of *AD* is also low.

The conditions under which Iseley, (10), did his work, probably prevented any attempt upon his part to estimate the age of the mus-sels used in his study. However, in the river form of this species, (*Quadrula rubiginosa*), he gives, (p. 10), the average yearly growth of 3 young specimens as an increase of 6.1% in length, 5.6% in height, 5.3% in breadth. From p. 11, an increase of 3% in these dimensions in two other specimens can be inferred, while 9.2% gain in length is deduced from the records of two additional specimens given on p. 12. It is unfortunate that none of the juveniles I had access to had quite reached the dimensions of the shells he used, but my results check with other investigators in that the rate of growth diminishes with age. Had it been possible to make a comparison on size alone, it would have been seriously discounted by the fact that lake dwelling shells are often depauperate. On the basis of the statement of authors cited, (2), that shells of the niggerhead and related species increase $\frac{1}{4}$ in. more or less in a year, my averages indicate in con-

trast, that up to 12 years the increase is more like an inch for this species.

In a related form, *Quadrula (Fusconaia) undata*, the last investigators cited give 15.8 mm. as the length of a pond raised specimen at the close of the second year. This checks fairly well with my estimate of 2 year specimens of *F. flava*, as well as does the increase in two years of .44 in. which equals 11.17 mm.

2. AMBLEMA PLICATA

No. Spec.	Age	L	DVD	DSD	PD	AD	PHL	AHL	TH.
3	2	2.13cm.	1.74cm.	1.05cm.	1.65cm.	.50cm.	1.21cm.	.50cm.	.144cm.
3	3	117%	115%	147%	115%	112%	111%	110%	111%
3	4	163%	152%	145%	163%	154%	150%	120%	200%
3	5	195%	186%	108%	200%	172%	182%	176%	166%
3	6	247%	250%	265%	271%	163%	200%	145%	225%
3	7	288%	280%	260%	300%	240%	290%	220%	270%
3	8	289%	260%	270%	301%	220%	262%	246%	298%
3	9	312%	284%	276%	300%	246%	300%	250%	222%
3	10	339%	319%	279%	398%	220%	348%	260%	244%
3	11	265%	244%	288%	280%	222%	244%	184%	285%
3	12	338%	328%	295%	360%	260%	350%	290%	235%
3	13	356%	332%	310%	381%	354%	362%	310%	290%
3	14	409%	364%	376%	440%	292%	390%	410%	444%
3	15	410%	362%	380%	454%	260%	4215%	356%	357%
3	16	403%	352%	368%	436%	286%	429%	332%	421%
Average growth per year in each dimension for 16 years.									
		166%	147%	142%	182%	104%	170%	125%	112%

DEDUCTIONS FROM TABLE OF PERCENTAGES AND REMARKS.

In this species, the dimensions of *L*, *PD*, and *PHL* increase most greatly with age. *DVD* and *DSD* increase at about the same rate. *TH* and *AD* show the least increase. Increase in size is continuous from year to year, but shells 14-15 years of age are as large as some older ones. From the ages 8-12, *DVD* and *DSD* increase more rapidly than in early years, as do also *PD* and *PHL*. While the increase in *TH* is relatively less, that in *AHL* is relatively more.

This species is most likely the one studied by Isely, (*Quadrula undulata*). In young specimens, (p. 10), he observed a gain of 21% in length, 20% in height, and 19% in breadth. In my specimens, the ones most corresponding with his in dimensions are aged 6, 8 and 9 years. My specimens for those years check up length 20%, height 22%, breadth, 1%. The small number of variants used might explain the greater discrepancy between these, or the fact that lake dwelling forms are usually smaller than river specimens, even earlier

in life. Isley also records, (p. 11), the growth of other specimens of this shell, the smallest of which most closely corresponds to the oldest of my material. Here the rate of growth obtained in the 3 dimensions in order is 15%, 10%, 11%. Using the shell dimensions composing the means for 15 and 16 years, I obtain 11%, 12% and 14% which allowing for environment seems fairly close. Coker, Shira, Howard and Clark, (2), studied *Quadrula plicata*, a closely related species. They report it 13.5 mm. in length at the close of the second year as reared in a pond. This is nearly a mm. smaller than my youngest specimen of *plicata*. They, however, recognize the fact that conditions of pond life are apt to produce stunting effects. They record another specimen which increase 5.17 in. in 2 yrs., 3 mos., 2 weeks. I find a similar increase in my specimens of *costata* between the ages of 2 and 4.

I find I can select a series of variants which will exhibit very nearly the same percentage of yearly increase as Isely's remaining data on *Q. undulata*, (p. 13). Isely found a specimen 48 mm. in length increased 13% in that dimension in one year; a 64 mm. specimen, 12%; a 70 mm. specimen, 107%; 72 mm., 108%; 82 mm., 103%. The ages of my material to which these correspond are 5, 9, 10, 10, and 14 years.

My results, as obtained by the method described, indicate that Isely's estimate of a yearly growth in length of from 5-25 mm. is somewhat conservative for one based on the smallest and youngest specimens. I find that by applying the average growth in length, it is at least 31 mm. in *lake* shells. Within the limits of my material, it seems probable that a length of 110-120 mm. could be reached at 15 years, as Isely found in the case of mussels from Shoofly Creek. Undoubtedly the environment is a very large factor in determining the rate of growth.

3. PLEUROBEMA COCCINEUM PAUPERCULUM

No. Spec.	Age	L	DVD	DSD	PD	AD	PHL	AHL	TH.
2	8	5.84cm.	4.47cm.	2.85cm.	4.8 cm.	.97cm.	3.12cm.	1.28cm.	.27cm.
2	9	105%	106%	103%	114%	140%	112%	103%	125%
2	10	114%	110%	120%	123%	114%	121%	146%	135%
2	11	115%	115%	109%	125%	174%	131%	111%	174%
2	12	119%	97%	111%	114%	160%	111%	104%	77%
Average growth per year in each dimension for 12 years, (oldest shell),									
		4.6%	2.5%	4%	6¼%	7½%	6¼%	9¼%	
Average growth per year in each dimension for 5 years, (8-12 yrs. inclus.)									
		11%	6%	9%	15%	18%	15%	15%	22%

DEDUCTIONS FROM TABLE OF PERCENTAGES.

As the few shells of the series obtainable were quite old, it is difficult to come to any satisfactory conclusion concerning their rate of growth, and I have felt that the best insight is obtained by presenting the results as I have above. Within the limits of these observations, growth appears more rapid in the following dimensions, *PD*, *AD*, *AHL*, *PHL*, and *TH*. It is relatively slower in *L*, *DVD*, *DSD*. Specimens may be larger at 10 years than some others at 12 years. Increase in thickness is most marked. The rate of growth in *PD*, *AD*, *AHL*, *PHL*, is nearly the same.

4. ELLIPTIO DILATATUS STERKII

No. Spec.	Age	L	DVD	DSD	PD	AD	PHL	AHL	TH.
1	2	2.09cm.	1 cm.	.5cm.	1.6 cm.	.45cm.	1 cm.	.3 cm.	.05cm.
1	3	123%	132%	142%	128%	113%	113%	150%	200%
2	4	226%	243%	292%	229%	222%	240%	240%	380%
2	5	246%	245%	300%	262%	206%	280%	273%	440%
2	6	215%	235%	292%	225%	193%	237%	250%	380%
4	8	342%	360%	450%	348%	300%	386%	350%	620%
4	9	342%	355%	448%	368%	277%	396%	403%	480%
4	10	370%	381%	480%	395%	260%	410%	423%	560%
4	11	385%	496%	570%	415%	313%	444%	433%	660%
4	12	381%	374%	556%	407%	322%	440%	533%	600%
Average growth per year in each dimension for 12 years.									
		144%	160%	219%	156%	108%	172%	179%	85%

DEDUCTIONS FROM TABLE OF PERCENTAGES AND REMARKS.

The greatest increase in the dimensions of this shell during the period indicated are to be found in *DSD*, *PHL*, *AHL*, and *Th*. Growth appears to be continuous through the years. *PD* and *DVD* increase at practically the same rate, while the increase in thickness is relatively large. Some of the shells are as large at 11 years as others are at 12. The rate of growth appears to be more rapid between the years 9-12 than years 4-8. This increase is not as well marked in *AD* as in other dimensions.

Authors cited, (2), record a growth of 4.3 mm. for a medium sized specimen, (*Unio gibbosus*), in a crate anchored in the Mississippi river in a period a little over 2 years, 3 month, (p. 127). This amount of growth, which is a yearly average of 2.2 mm., is found in my specimens between the ages of 4-5, 8-9, 9-10, 11-12.

5. *LASMIGONA COSTATA ERIGANENSIS*.

No. Spec.	Age	L	DVD	DSD	PD	AD	PHL	AHL	TH.
2	6	7.41cm.	4.05cm.	2.59cm.	5.50cm.	1. 9cm.	3.62cm.	1. 7cm.	.21cm.
2	7	101%	105%	106%	105%	90%	109%	94%	124%
2	8	113%	118%	113%	114%	116%	85%	205%	109%
2	9	112%	113%	113%	108%	95%	122%	103%	124%
2	10	114%	114%	106%	117%	111%	124%	91%	100%
Average growth per year in each dimension for 10 years, (oldest shell),									
		4%	5%	4%	4.4%	1.6%	4%	9.2%	7.6%
Average growth per year in each dimension for 5 years, (6-10 yrs. inclus.)									
		10%	12½%	9½%	11%	4%	10%	23%	19%

DEDUCTIONS FROM TABLE OF PERCENTAGES.

As the few shells of the series obtainable are somewhat advanced, it is not easy to draw satisfactory conclusions concerning their rate of growth. However, *DVD*, *PHL* and *TH* increase most rapidly, the large increase in *AHL* is probably accidental. Increase in thickness is not so well marked.

6. *ANODONTA GRANDIS FOOTIANA*

No. Spec.	Age	L	DVD	DSD	PD	AD	PHL	AHL	TH.
1	4	5.27cm.	3.27cm.	2.24cm.	3. 6cm.	1.65cm.	2. 3cm.	1. 3cm.	1.4cm.
1	5	142%	127%	143%	144%	140%	130%	138%	107%
3	6	175%	165%	174%	169%	138%	184%	169%	157%
3	7	166%	151%	156%	175%	145%	170%	147%	121%
3	8	160%	150%	133%	166%	148%	112%	137%	128%
3	9	163%	170%	180%	196%	168%	184%	160%	128%
Average growth per year in each dimension for 9 years, (oldest shell),									
		34%	29%	32%	39%	27%	31%	28%	16%
Average growth per year in each dimension for 5 years, (5-9 inclus.)									
		61%	53%	57%	70%	48%	56%	50%	28%

DEDUCTIONS FROM TABLE OF PERCENTAGES AND REMARKS.

The greatest increase in the years represented is in the dimensions of *PD*, *DSD*, *PHL*. The latter appears to enlarge uniformly. It is noted that shells may be as large at 6 years as at 9; the relative increase in thickness is apparently small. Isely, (10, p. 15), made studies of the parent species *A. grandis*. The nearest specimen to his I studied and no larger one, was aged 9 years. It showed an increase of 3% in length, 20% in height, and 47% in breadth over the average for 8 year specimens, against 4%, 3.2% and 6.7% in Isely's specimens. The tremendous increase in inflation is undoubtedly due to the lake environment, the greater height of my specimen seems to be that of an unusual variant, since the height Isely gives may be obtained in my material by selection of the variants.

7. LEPTODEA (PARAPTERA) FRAGILIS.

No. Spec.	Age	L	DVD	DSD	PD	AD	PHL	AHL	TH.
1	3	4.44cm.	3.14cm.	1.44cm.	3	cm.	1. 1cm.	2. 2cm.	1. 2cm. .9cm.
2	4	125%	114%	131%	125%	145%	118%	110%	128%
2	5	220%	202%	218%	252%	201%	222%	170%	166%
4	6	203%	195%	216%	220%	218%	222%	175%	144%
4	7	208%	227%	230%	233%	213%	216%	176%	177%
4	8	201%	196%	203%	215%	223%	221%	170%	188%
4	9	191%	189%	148%	213%	190%	192%	157%	155%
4	12	290%	256%	262%	316%	309%	325%	250%	244%
Average growth per year in each dimension for 12 years.									
		61%	57%	59%	73%	67%	68%	42%	42%

DEDUCTIONS FROM TABLE OF PERCENTAGES AND REMARKS.

Growth increase appears most rapid in *PD*, *AD*, and *PHL*; least in *AHL*, *TH*. Increase is at the same rate in *L*, *DVD*, *DSD*, while according to this data, growth is greatest at 12 years, increasing steadily up to this period. *DVD*, *AD*, *PHL* and *TH* apparently grow the most rapidly in the years 7-9, inclusive. *PD*, however, increases most rapidly years 4-6 inclusive.

Two related species, *Lampsilis gracilis* and *Lampsilis laevissima*, have been observed by authors cited, (2). They found the first named of these species to increase 190% in length in one year. By my data, such a specimen would be between 11-12 years. The second is cited as one of the "paper shells," increasing $\frac{1}{2}$ to 2 in. per year, (12.7 to 50.80 mm.), in length. The latter represents in its lower ranges the amount of increase found among my shells.

8. PROPTERA ALATA

No. Spec.	Age	L	DVD	DSD	PD	AD	PHL	AHL	TH.
1	2	1.28cm.	.85cm.	.35cm.	.85cm.	.33cm.	.55cm.	.45cm.	.05cm.
1	3	112%	120%	120%	117%	121%	136%	78%	140%
1	5	105%	105%	105%	105%	136%	118%	180%	90%
1	6	257%	320%	328%	241%	379%	309%	363%	120%
1	7	201%	247%	240%	202%	267%	245%	133%	100%
1	8	371%	461%	554%	417%	369%	481%	255%	220%
2	9	384%	473%	520%	423%	363%	473%	233%	240%
2	10	511%	623%	780%	541%	560%	563%	493%	480%
1	12	703%	854%	1017%	764%	757%	927%	377%	700%
1	13	668%	755%	871%	741%	681%	836%	365%	600%
2	14	523%	600%	745%	568%	576%	636%	300%	400%
2	15	859%	854%	1128%	930%	1072%	1178%	471%	880%
1	16	750%	820%	911%	823%	785%	909%	377%	500%
1	20	812%	840%	1148%	930%	757%	1054%	400%	640%
1	22	788%	794%	837%	811%	694%	863%	366%	480%
Average growth per year in each dimension for 22 years.									
		260%	294%	364%	282%	280%	324%	129%	190%

DEDUCTIONS FROM TABLE OF PERCENTAGES.

The greatest increase of any of these dimensions is seen to be in *DSD* and *PHL*. While an increase is noted throughout the years, it is nearly uniform in *PD*, *AD*, and *DVD*, and rather large in *TH*. Growth is most rapid between 12-16 years, when it is especially noticeable in *L*, *DVD*, *TH*, *DSD*; less so in *AHL*.

9. ANODONTOIDES FERRUSSACIANUS SUBCYLINDRACEOUS

No.	Spec.	Age	L	DVD	DSD	PD	AD	PHL	AHL	TH.
2	3		4.78cm.	3. 1cm.	1.65cm.	3.67cm.	1. 1cm.	2.02cm.	.93cm.	.08cm.
2	4		111%	115%	121%	111%	111%	124%	113%	120%
3	5		128%	99%	136%	135%	134%	133%	134%	137%
3	6		140%	108%	149%	150%	138%	154%	136%	147%
3	7		145%	113%	147%	148%	140%	163%	146%	187%
3	8		151%	119%	163%	141%	172%	123%	200%	187%
1	9		162%	121%	180%	150%	200%	148%	155%	175%
Average growth per year in each dimension for 9 years,			26%	8%	33%	26%	33%	27%	32%	39%

DEDUCTIONS FROM TABLE OF PERCENTAGES.

Increase with age is most marked in *DSD*, *AD*, *TH* and *AHL*. All dimensions grow more rapidly between 6-9 years than between 3-6. Increase in height, *DVD*, is little; growth of *L*, *PD*, *PHL* is uniform, that of thickness, rapid. This shell is one which is rarely found in large rivers.

10. LIGUMIA, (LAMPSILISP RECTA.)

No.	Spec.	Age	L	DVD	DSD	PD	AD	PHL	AHL	TH.
1	9		6. 1cm.	2. 3cm.	1.45cm.	4. 8cm.	1.13cm.	3. 1cm.	85cm.	.15cm.
2	10		155%	200%	170%	150%	185%	180%	167%	226%
2	11		146%	166%	168%	141%	172%	150%	188%	206%
2	12		146%	167%	165%	141%	184%	150%	176%	206%
1	13		178%	193%	190%	182%	185%	201%	188%	146%
1	14		191%	191%	213%	191%	222%	235%	200%	306%
2	15		148%	153%	182%	145%	177%	170%	170%	200%
2	16		182%	169%	211%	186%	195%	191%	190%	200%
1	17		155%	211%	209%	185%	146%	229%	192%	226%
1	18		170%	174%	200%	176%	160%	190%	153%	246%
Average growth per year in each dimension for 18 years,			57%	72%	81%	59%	74%	79%	72%	106%

DEDUCTIONS FROM TABLE OF PERCENTAGES AND REMARKS.

Within the limits of the ages represented, it seems clear that *DVD*, *DSD*, *PD*, *PHL*, and *AHL* increase most rapidly with age. The rate is greater in *TH*; *L* and *AD* have apparently the same rate of growth, while the remaining dimensions, with the exception of *TH*,

grow largely at the same rate. It is observed that some specimens are as large at 14 as at 18 years.

The preceding observations are based largely on the averages, but a comparison of from age to age of the above percentages indicates that *DSD* increases steadily throughout, as well as *PHL* and *PD*. *AD* seems to relatively diminish with the years, while in later ones, *PD*, *DVD*, and *DSD* tend to increase relatively more rapidly than the length. The rate of growth of the hinge lines is approximately the same. Certain specimens reach a maximum growth earlier than others.

Of the 19 species of Unionidae studied by authors cited, (2), the greatest growth for a period a little over 2 years, 3 months, was observed in a medium sized example of this species. The gain in that period was 44.7 mm. in one specimen alone, a yearly average of 2.23 cm. Referring to my data, I find even a greater growth between the ages of 9-10, 11-12, 15-16.

11. LAMPSILIS (LUTEOLA) SILIQUOIDEA ROSACEA.

No. Spec.	Age	L	DVD	DSD	PD	AD	PHL	AHL	TH.
1	6	5.12cm.	3 cm.	1.83cm.	3. 8cm.	1. 3cm.	2.35cm.	1 cm.	.20cm.
2	7	110%	108%	74%	108%	115%	119%	112%	130%
2	8	106%	110%	116%	102%	117%	123%	122%	120%
2	9	111%	120%	121%	113%	113%	138%	122%	145%
3	10	134%	136%	146%	142%	137%	144%	196%	160%
3	11	142%	140%	151%	147%	128%	162%	156%	170%
3	12	155%	151%	265%	160%	146%	171%	190%	210%
3	13	107%	119%	117%	126%	108%	119%	156%	251%
3	14	161%	154%	171%	166%	147%	183%	163%	180%
3	15	144%	143%	148%	150%	130%	181%	156%	190%
3	16	147%	135%	186%	185%	123%	175%	158%	175%
2	17	167%	155%	172%	171%	158%	204%	180%	210%
2	18	152%	148%	176%	158%	146%	180%	178%	215%
1	19	167%	158%	164%	171%	161%	172%	185%	170%
Average growth per year in each dimension for 19 years.									
		26%	25%	42%	32%	21%	41%	40%	54%

DEDUCTIONS FROM TABLE OF PERCENTAGES AND REMARKS.

Throughout the life of the animal, as illustrated in the above series, growth is most rapid in *DSD*, *PD*, *PHL*, *AHL* and in *TH*. Specimens may be as large at 17 years as at 19. Thickness exhibits the most outstanding increase. According to these results, the shell grows somewhat more rapidly after twelve years than in the six preceding ones, the thickness nearly doubling. *L*, *DVD*, *DSD* grow largely at the same rate.

This species of mussel is of considerable commercial importance,

and its rate of growth has been studied in greater detail than in any other mussel. Coker, Shira, Howard and Clark, (2), record its growth as follows, p. 126.

Age	Length	% Increase
2	43.4mm.	
3	68.8mm.	158%
4	77 mm.	177%
5	80.6mm.	180%
6	84.9	170%

Howard, (9), p. 70, records even a greater average increase in length from mussels reared in a floating crate—209%. My youngest L. Erie specimen was 6 years old and had a length of 51.2 mm. against 84.6 mm. for those from the Upper Mississippi River. However, it is well known that the lake forms of this species, as will be taken up in detail later, are unusually depauperate when compared with those from the Mississippi. The average rate of growth calculated from their data is 62%, while between the years 6 and 7, I record a minimum of 82%.

12. LAMPSILIS OVATA CANADENSIS

No. Spec.	Age	L	DVD	DSD	PD	AD	PHL	AHL	TH.
2	4	1. 9cm.	1.29cm.	.74cm.	1.28cm.	1.22cm.	.67cm.	.42cm.	.12cm.
2	7	332%	339%	400%	336%	164%	400%	352%	183%
2	8	272%	276%	332%	273%	137%	310%	305%	133%
4	9	317%	360%	480%	479%	155%	388%	326%	208%
4	10	340%	372%	425%	343%	152%	417%	262%	191%
4	11	350%	400%	423%	365%	170%	440%	356%	250%
4	12	423%	466%	509%	453%	190%	552%	373%	291%
4	13	378%	390%	463%	406%	163%	485%	395%	300%
4	14	418%	461%	520%	453%	173%	522%	380%	308%
4	15	426%	482%	573%	484%	178%	609%	440%	333%
4	16	460%	509%	556%	476%	212%	606%	440%	308%
1	17	503%	527%	635%	541%	210%	716%	416%	350%
1	19	515%	529%	623%	586%	188%	619%	511%	366%
Average growth per year in each dimension for 19 years.									
		186%	206%	249%	210%	47%	256%	187%	106%

DEDUCTIONS FROM TABLE OF PERCENTAGES AND REMARKS.

The average increase is most marked in the dimensions of *DVD*, *DSD*, *PD*, *PHL*, growth in *AD* being less. Growth appears to be somewhat irregular, some specimens being larger at an early age than others. *TH* increases consistently with age, and the rate of growth of *DSD*, *TH*, and *PHL* is most similar. Growth appears to be greater in years, (7-11), than in later ones, (12-16). During the latter period, however, growth in thickness is most rapid, *PHL* markedly more, *AD*, *L*, and *AHL* relatively less.

Coker, Shira, Howard and Clark, (2), report that this species attained a length of 41-47 mm. in two growing seasons, 65 mm. by August of the third growing season. Specimens 45-47 mm. in length, evidently in the second year of free life, were measured and planted in the Mississippi river by Lefevre and Curtis. When recovered by the former authors, they had attained a length of 81-85 mm. None of my specimens were so large at 4 years, the nearest corresponding being at 7-8 years, while the nearest specimen attaining a length of 81-85 mm. were between 12-13 years of age. Here again the environment may exercise a deterrent effect upon growth. The average increase in length of the specimens described by these authors—90%—is far lower than the one I have derived.

TABLE OF AVERAGES INDICATING COMPARATIVE GROWTH OF SPECIES STUDIED.

	Total shells examined	No. years basis of average	Calculated increase in length per year, MM.	Average Yearly Increase in Dimensions							
				L	DVD	DSD	PD	AD	PHL	AHL	TH
<i>Fusconaja flava parvula</i>	34	12	5 mm	143%	150%	209%	161%	110%	192%	116%	87%
<i>Amblema plicata costata</i>	45	16	8.3mm	166%	147%	142%	182%	104%	170%	125%	112%
<i>Pleur. coccin. pauperculum</i> ...	10	12	2.7mm	4.6%	2.5%	4%	6¼%	7½%	6¼%	6¼%	9¼%
<i>Elliptio dilatatus sterkii</i>	28	12	7.1mm	144%	160%	219%	156%	108%	172%	179%	285%
<i>Lasmigona costata eriganensis</i>	10	10	3.1mm	4%	5%	3.8%	4.4%	1.6%	4%	9.2%	7.6%
<i>Anodonta grandis footiana</i> ...	14	9	8.7mm	34%	29%	32%	39%	27%	3%	28%	16%
<i>Leptodea fragilis</i>	22	12	10mm.	61%	57%	59%	73%	67%	68%	42%	42%
<i>Proptera alata</i>	19	22	7.9mm	260%	294%	364%	282%	280%	324%	129%	190%
<i>Anodontoides feruss. subcyl.</i>	17	9	8.2mm	26%	8%	33%	26%	33%	27%	32%	39%
<i>Ligumia recta</i>	15	18	6.3mm	57%	72%	81%	59%	74%	79%	72%	106%
<i>Lampsilis siliquioidea rosacea</i>	35	19	5.7mm	26%	25%	42%	32%	2.1%	41%	40%	50%
<i>Lampsilis ouata conadensis</i> ..	40	19	5.4mm	186%	206%	249%	210%	47%	256%	187%	106%

The following is evident from the preceding table as to the average growth per year in the different groups of mussels, with regard to the dimension of length:

Hard shell, slow growing *Quadrula* mussels,

(species 1, 2, 4)..... 6.8 mm. or .27 in.

Paper or thin shell, rapid growing mussels,

(species 6, 7, 9)..... 9 mm. or .36 in.

Intermediate or *Lampsiline* group mussels,

(species 8, 10, 11, 12)..... 8.2 mm. or .33 in.

The numbers of shells in the series representing *Pleurobema* and *Lasmigona*, were too small to be taken into consideration in this comparison. Comparing with the data cited from Coker, Shira,

Howard and Clark, (2), it is evident that my data checks only with their observations for the *Quadrulas*, the average of growth for the remaining groups being considerably less.

VI.—CORRELATIONS.

From the tables of percentages calculated for each species, the following correlations may be derived as to the growth of the different regions of the juvenile shell:

1. Greater degree of inflation, *DSD* is associated with less dorsal ventral diameter, (*DVD*), (height), in all the species.
2. In all but three species, (to which there are exceptions), there is a greater degree of inflation, (*DSD*), associated with greater posterior development of the shell, *PD*. The exceptions are *Pleurobema*, *Ligumia*, and *Anodontoidea*.
3. In all but three species, (to which there are exceptions) greater *PD* is associated with greater *PHL*.
4. Greater *DSD*, *PD*, *PHL* and less *DVD* are associated with less *TH* in all species excepting *Pleurobema*, *Elliptio*, *Lasmigona*, *Anodontoidea*, *Ligumia*, and *Lampsilis siliquioidea*.
5. These correlations of growth in juvenile shells are found to be very similar to those obtained from measurements of adult shells, (7, p. 173).

VII.—CONCLUSIONS.

In addition to the data already presented as to the rate of growth in the different species, we may add the following conclusions to be derived, viz.:

1. Fresh water mussels dwelling in lakes, like their river relatives, grow most rapidly in the earlier years of their lives, and the process of growth slows down considerably with advanced age. It must be remembered in this connection that none of the shells reported upon had reached an extreme old age.
2. The rate of growth is highly variable, even in mussels of the same species.
3. With the possible exception of the mussels of the *Quadrula* group, lake dwelling mussels as a rule grow more slowly than those from rivers, at least with regard to the dimension of length.
4. The growth of juvenile shells of the species discussed exhibit mostly the same correlation in growth of parts as do the adult shells.

VIII.—SUGGESTIONS AS TO CAUSES OF FACTS.

Allusion has been continually made to the depauperate quality of many lake shells, so for the most part the results as obtained in the "paper" and *Lampsiline* groups of shells are those which would have been expected. In a previous paper, (5), I have been able to show that the thickness of shell of mussel species from L. Erie is negatively correlated with the percentage of calcium carbonate in the water, whereas in the Upper Ohio River Drainage, a positive correlation exists. L. Erie water, besides containing more calcium carbonate, contains greater quantities of other alkaline substances. The substances mentioned appear to act in such a way as to prevent less absorption of calcium carbonate by the L. Erie shells than by those of the Upper Ohio; as a consequence the L. Erie shells are thinner.

It has also been previously stated that a convenient index to the rate of growth of a mussel lies in the rate of growth of its shell. Although length has been the common dimension by which the rate of growth has been estimated, and while thickness of the shell is the characteristic which may be associated with the amount of calcium carbonate in the water, it seems plausible to assume that the inorganic salts in L. Erie water may through favoring the development of a thinner shell, cause a corresponding inhibition of the development of other parts of the shell architecture, the reaction of the mussel being to maintain the "biological balance" of the different parts. This seems best illustrated with the results of the *Quadrulas* in L. Erie. They are always slow growers, and develop a thick shell. However, in L. Erie they have a thinner shells, so if growth in length is in pace with that of the shell, it seems to be at the expense of thickness. Under this combination of circumstances, the shell may take from the water, just what it needs in the way of lime—a point which is in accord with our knowledge of the absorption of inorganic salts by living shells.

An interesting example in connection is that of *Lampsilis*, (*luteola*) *siliquoidea* which in Lake Erie develops into a thin and dwarfed shell. Yet in Lake Pepin, an expansion of the Mississippi river in southern Minnesota, which possibly presents all lake characteristics cited for L. Erie, except the high mineral content of the water, this species reaches its maximum size and development.

With regard to the exceptions in the general trend of the correlations as presented for certain species, the cases of *Pleurobema* and *Lasmigona* are difficult to comment upon on account of the small amount of material. Nor am I able to add anything for the other species furnishings exceptions to the general trend of correlations beyond suggestions presented in another paper, (7, p. 174), beyond stating the results may have been occasioned by unusual variants.

The fact that juvenile shells exhibit mostly the same correlations as adult shells may indicate that the lines along which they develop are largely predetermined. Predetermination in this case, however might indicate a sufficiently rigid uniformity of environmental conditions to guide the shells in their development along the lines of their ancestors, or the inherent nature of the mussel protoplasm itself.

IX.—POSSIBLE SOURCES OF ERROR.

It is true that in the experiments dealing with mussel culture I have cited, that all the shells were subjected to identical environmental conditions, which in itself probably insures a greater uniformity of results for the types of environment studied. A small amount of the material needed to obtain as complete a series as possible came from other localities in L. Erie besides Presque Isle, the source of most of it. There need be raised on this account no serious objection as from the aspect of environmental effects upon shells, the broad idea of the lake environment being more important in the present discussion than that of any separate effects of the smaller localities involved in it. If anything, it is more probable that greater balance has been given the calculations on account of some of the material being from different localities.

Undoubtedly the results would be more satisfactory to some, if it had been possible to compare equal numbers of shells in all cases, but the results obtained have so fitted in with what was previously known of the growth process in these animals, that it is felt no serious objection can thereby be interposed.

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CORRECTION:—The table of absolute minimum temperatures of the last issue (Vol. VIII, Nos. 4, 5, July-September, 1922), gives 17 degrees above zero for January, 1918, and 11 degrees above for January, 1919. Both of these should read "below zero," or minus 17 and minus 11. See page 123.